Received: 10 April 2022 | Revised: 12 March 2023 | Accepted: 23 May 2023

DOI: 10.1111/geb.13714

RESEARCH ARTICLE

Global Ecology and Biogeography A Journal of Macroecology WILEY

Two centuries of spatial and temporal dynamics of freshwater fish introductions

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Funding information
Austrian Science Foundation FWF, Grant/Award Number: I 4011-B32; Bundesministerium für Bildung und Forschung, Grant/Award Number: 16LC1807A; Deutsches Zentrum für integrative Biodiversitätsforschung Halle-Jena-Leipzig, Grant/Award Number: DFG FZT 118 – 202548816; Ministerio de Ciencia e Innovación, Grant/Award Number: CGL2016-80820-R, FJCI-2016-30829, PID2019-103936GB-C21, RED2018-102571-T and TED2021-129889B-I00

Handling Editor: Volker Bahn

Abstract

Aim: Investigating major freshwater fish flows (translocations) between biogeographic regions and their temporal dynamics and also quantifying spatial patterns and temporal changes in the array of introduced species, and the emergence and distance between major donor and recipient regions.

Location: Global.

Time Period: 1800–2020.

Major Taxa Studied: Freshwater fishes.

Methods: We analysed a global dataset on freshwater fish introductions (4241 events of 688 species). Freshwater fish flows were investigated with flow diagrams and χ^2 tests, while PERMANOVA (permutational multivariate analysis of variance) was used to test the association between species and regions and temporal shifts. Cluster analysis revealed major recipient areas and composition of the introduced species. Finally, changes in distances between donor and recipient sites were tested with PERMANOVA.

Results: The number of introductions between biogeographic regions mirrored the European and North American dominance before World War II (WWII) and the trends in recreational fishing, biocontrol programmes and food production, especially in the Sino-Oriental region, which has a long tradition of aquaculture and fishkeeping. Over the years, the origins and composition of introduced species changed uniquely in each biogeographic region, although the most introduced species are common to every region. Salmonids and other cold-water species were frequently introduced before the 1950s, whereas tropical ornamental and aquaculture species currently prevail. Distances between donor and recipient sites did not vary over the time. After WWII, the Sino-Oriental region consolidated its dominance and the Ethiopian and Neotropical regions emerged as new global donor and recipient regions.

Main Conclusions: Global policy should focus on tropical ornamental and aquaculture species, which could benefit from global warming, especially in the Sino-Oriental region, because it currently dominates freshwater fish species flows, and the Ethiopian and Neotropical regions, because they recently emerged as important global donor and recipient regions of freshwater fish introductions.

KEYWORDS
biogeographic region, freshwater ecosystem, geographic distance, introduction pathway, invasive alien species, species origin

1 | INTRODUCTION

Human agency has broken down biogeographic barriers and re-distributed species across the globe (Capinha et al., 2015; Dawson et al., 2017). Over time, species introductions have increased alongside human population growth and technological advances which, for example, allowed transporting live freshwater fishes across the globe (Chapman et al., 2017; Seebens, 2019; Stevens et al., 2017). Therefore, flows (translocations) of species from their donor to recipient regions should be largely explained by human colonization patterns and current or past trade networks and socio-economic trends (Chapman et al., 2017; Lenzner et al., 2018; Olden et al., 2021).

Historically, the Palearctic and the Sino-Oriental regions, primarily China, have been the main global donors and recipients of alien species (Bernery et al., 2022; Lenzner et al., 2018; Su et al., 2020). These regions hosted several historical empires, the Chinese in the East and the Roman in the West, where a number of animal species were domesticated and redistributed (Toussaint et al., 2018). One famous example of early aquaculture is the domestication of the common carp (*Cyprinus carpio*). This species has experienced a human-induced expansion across Europe and China that began more than thousand years ago (Balon, 1995; Ma et al., 2003; Mitchell, 2009) and has become one of the worst invasive species worldwide (Lowe et al., 2000). Brown trout (*Salmo trutta*) is, by contrast, a more contemporary example of a global freshwater fish invader that has a current distribution largely reflecting the former British Empire (McIntosh et al., 2011). Nevertheless, as new economic centres emerged, historical introduction hubs and main donor and recipient areas were replaced by new major donor and recipient regions in developing countries (Haubrock et al., 2022). Advancing our understanding of spatial and temporal introduction patterns of freshwater fishes is essential for basic science and for designing policies and monitoring programmes alike (Chapman et al., 2017). However, despite the remarkable studies on the topic (e.g., Toussaint et al., 2014, 2016), we lack a comprehensive exploration of the major donor and recipient biogeographic regions of freshwater fish species, and how species flows have changed over time.

Freshwater organisms such as fishes face major spread barriers between catchments, resulting in inferior long-distance dispersal capabilities compared with marine or terrestrial species (Dias et al., 2014). In accordance, the main introduction pathways (Hulme et al., 2008) for freshwater fishes have been related to specific activities and to species that fulfil particular human needs, although fish can spread to formerly inaccessible river basins when artificial canals are built (i.e., corridor introduction pathway followed by unaided dispersion; Leuven et al., 2009). Freshwater fish introductions have been dominated by releases and escapes related to fisheries enhancement, sport fishing, aquaculture and, much more recently, fishkeeping (Arlinghaus et al., 2015; Chan et al., 2020; Ellender et al., 2014). The restricted number of introduction pathways and target stakeholders may be considered advantageous for focussing management activities. However, the relevance of individual drivers of fish introductions and the associated species have likely changed over time (Essl et al., 2015). For example, recreational fishing tends to increase with economic development of countries, but then decrease in highly urbanized societies (Arlinghaus et al., 2015). By contrast, the ornamental fish trade and, especially, aquaculture have exhibited a steep global growth in recent decades (Chan et al., 2020). Aquaculture is expected to grow further to feed the rising human population (Reid et al., 2019), especially in developing countries (Haubrock et al., 2022). Consequently, knowing which species are gaining prominence and which regions have become major donors and recipient centres in different periods is of major importance to narrow down monitoring programmes and prevention protocols.

Here, we used FishBase (Froese & Pauly, 2022), one of the most comprehensive databases on fish introductions (Casal, 2006; Maldonado et al., 2015; Ruesink, 2005), to provide a detailed analysis of global freshwater fish introductions. Specifically, we identified (i) the major freshwater fish flows between biogeographic regions and how they varied during the last c. 200 years, (ii) changes in the composition of species being introduced and the association between species and regions over time, and (iii) the emergence of new global donor and recipient regions and the characteristics of the species introduced in each region. To undertake these tasks, we analysed the frequency and species composition of exchanges among freshwater fish regions, and their changes over time. We then analysed how the frequency of introductions in each region and composition of introduced species have changed and determined periods with homogeneous introduction rates and species. We identified trends and introduction centres (i.e., clusters) of distinct biogeographic origin during these periods. Finally, we investigated changes in the distances between donor and recipient regions.

2 | METHODS

2.1 | FishBase dataset

We accessed FishBase (www.fishbase.org), a global information system which contains 34,800 fish species, by February 2021. We retrieved data on 4241 records involving 688 species (subspecies were not considered). One or multiple native freshwater fish biogeographic regions, namely Australian, Ethiopian, Madagascan, Nearctic, Neotropical, Palearctic and Sino-Oriental (Leroy et al., 2019), were assigned to each species based on a 2019 update of the dataset provided by Tedesco et al. (2017) ($n_{\text{known native regions}}=688$). In addition, we obtained the introduction date ($n_{\text{date}}=2676$; 63.1%), and donor ($n_{\text{donor site}}=2338$; 55.1%) and recipient sites and/or coordinates ($n_{\text{recipient site}}=4234$; 99.8%) from FishBase. Available information varied for each record, and as a consequence, the number of records that could be used varied among the different analyses (see section 1 in Supplementary material S1 for further information on data availability). For missing information on coordinates, we designated the site coordinates using Google Earth at the highest possible resolution (country, basin, river/lake, or site) when the toponymy was indicated. These specific coordinates were used to assign each recipient region to the corresponding freshwater fish region based on those depicted in Figure 1, which corresponded to Leroy's freshwater fish regions (Leroy et al., 2019). Reported years of introduction ranged from 1186 to 2014; when introduction dates were given as a range (e.g., 1980–1989) ($n_{\text{date as range}}=480$; 11.3%), we used the midpoint in the analyses. To investigate the associations between recipient freshwater fish biogeographic regions and species native regions, we used the data with known recipient sites ($n_{\text{recipient site}}=4234$). For specific analyses of changes in spatio-temporal introduction patterns, we

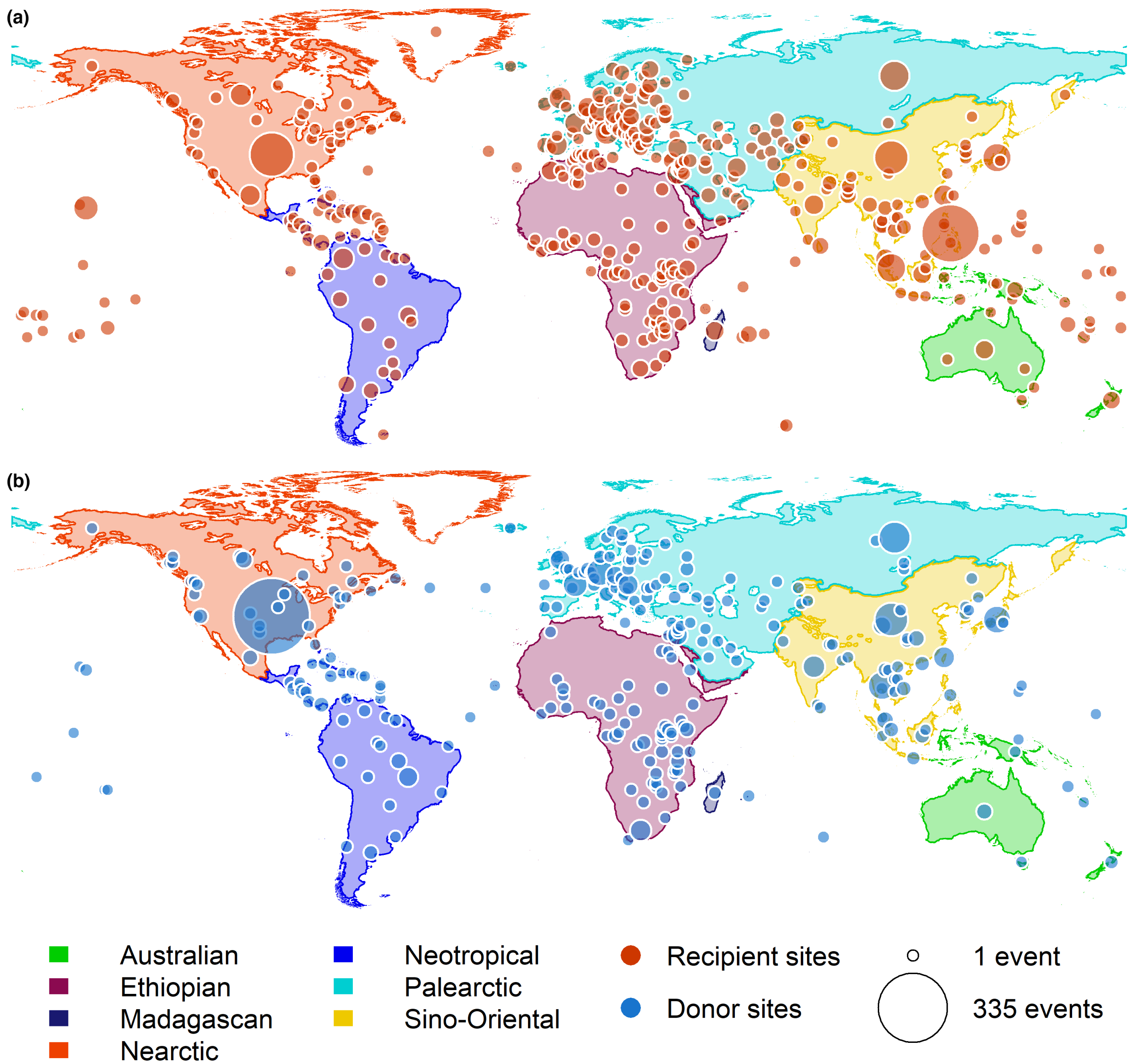

FIGURE 1 Biogeographic regions and recipient (a) and donor (b) locations available in the FishBase dataset (coordinates of the locations were obtained at the highest available resolution: country, basin, river/lake or site). The sizes of the circles are proportional to the number of introductions in each location. A figure connecting donor and recipient sites can be found in Supplementary material S1 (Figure S2).

restricted data to introduction years from 1800 onwards, as data on introduction events are scarce and highly uncertain prior to this date (25 entries were discarded; Hulme et al., 2008; Seebens et al., 2017, 2018). The number of records with available data for date of introduction and recipient site was 2651, whereas the number of records with known date and donor and recipient site was 1998.

2.2 | Data analyses

2.2.1 | Species transfers between biogeographic regions

We used flow diagrams to visualize species exchanges between biogeographic regions (i.e., total number of events including repeated introductions of the same species) using the *R* package *circlize* (Gu et al., 2014). While the recipient biogeographic region was based on the reported coordinates (see Figure 1a), the donor region was that of the native range of the species. For species with a native range spread across multiple biogeographic regions, we divided the introduction record across regions. Therefore, each species introduction value summed up to one, giving equal contribution of native range regions as donors in this analysis (e.g., each Northern pike *Esox lucius* record, which is a Holarctic species, was split as 0.5 Nearctic and 0.5 Palearctic origins).

The dataset retrieved from FishBase included successful introductions (those resulting in self-sustaining established populations), unsuccessful introductions (those that require continuous restocking to persist) and introductions for which establishment success is unknown. As we focussed on introduction routes and rates, rather than on subsequent invasion stages, we made no distinction between these groups. Nevertheless, Mantel tests indicated no statistical differences in species origin, frequency of introduction, and recipient regions between the successful, unknown and unsuccessful datasets (see section 2 in Supplementary material S1).

A flow diagram without repeated introductions of the same species can be found in section 3 of Supplementary material S1.

2.2.2 | Association between introduced species and biogeographic regions

To investigate the association between biogeographic regions and introduced species, we calculated the total number of introductions per species and region and used a χ^2 test. We used an undirected graph, depicted using the Fruchterman–Reingold algorithm (Fruchterman & Reingold, 1991), to display the similarities between biogeographic regions based on the resulting communities (i.e., introduced species in each region and frequency of these events) and the inverse distance between them (1—Bray–Curtis dissimilarity). Then, we calculated the proportion of species introduced in one single region (considering only one record per species) and their origins to investigate the degree of exclusivity among recipient biogeographic regions (i.e., species that have been solely introduced to one single biogeographic region). We used the size of the vertices in the graph to highlight the total number of species introduced in each region and used pie charts to depict the percentage of exclusive species and their origins. We finally inspected the proportion of introductions per biogeographic region of the 24 most frequently introduced species worldwide. The χ^2 test was carried out in *R* (R Development Core Team, 2021), and we used *vegan* (Oksanen et al., 2019) to calculate the Bray–Curtis dissimilarity between communities (species and number of events) introduced in each biogeographic region. The undirected graph was developed using *igraph* and *qgraph* (Csardi & Nepusz, 2006; Epskamp et al., 2012).

2.2.3 | Changes in spatio-temporal introduction patterns

Identification of temporal breakpoints and stability of species flows between biogeographic regions

We divided the study period (*c*. 200 years) into few shorter intervals to further investigate changes in species flows, species composition and major spatial introduction centres over time. We calculated the cumulative number of introduced species per year (1800–2011) for the 49 combinations of regions (as donors and recipients; see Figure S7 in Supplementary material S1). Then, we used segmented regression (Muggeo, 2003), as implemented in the *R* package *segmented* (Muggeo, 2008), to investigate the potential existence, evaluated employing the root mean squared error (RMSE), of different breakpoints (number and timing) in the frequency of introductions in these 49 species flows. Segmented regression is a piecewise linear regression that allowed us to break the independent variable (i.e., year) into smaller segments of homogeneous slope to better predict the response variable (i.e., number of introductions between biogeographic regions). Simultaneously, we calculated the Bray–Curtis dissimilarity matrix between the array of species introduced each year, and their number of introductions, and divided the resulting matrix accounting for the temporal order in the matrix with the breakpoints used for segmented regression. The cohesion and separation of the communities delineated by these breakpoints was evaluated employing the silhouette index (Arbelaitz et al., 2013; Rousseeuw, 1987) using the *R* package *cluster* (Maechler et al., 2022).

To deal with these conflicting objectives (number of breakpoints, RMSE and silhouette index) and find proficient interpretable breakpoints (number and position), we carried out a multiobjective optimization using the nondominated sorting genetic algorithm (NSGA-II; Deb et al., 2002) implemented in the *R* package *nsga2R* (Tsou, 2022). Multiobjective optimizations generate a series of breakpoints for whom improving the solution in a given objective reduces the performance in at least another objective (Gunantara, 2018). Among the generated solutions, we selected the one minimizing the number of breakpoints and RMSE and maximizing the silhouette index, giving equal importance to each one to balance the trade-off among competing objectives (Gunantara, 2018). See section 4.2 in Supplementary material S1 for further information about the multiobjective optimization.

Trends in introduction rates of the most frequent species

We used the number of fish introductions every 5 years to identify periods of low and high numbers of introduction events in each biogeographic region. In addition, we compared reported dates to investigate changes in the frequency of introduction of the most frequently introduced species during each period. Finally, we applied PERMANOVA (permutational multivariate analysis of variance; Anderson, 2001), to the Bray–Curtis dissimilarity matrix, to test whether the species composition and the number of introductions of these species depended on time and varied for each biogeographic region. We performed the PERMANOVA using the function *adonis2* (*permutations* = 9999), implemented in *vegan*, because introduction year was continuous.

Identification of spatial introduction centres with cluster analysis

We used cluster analysis to identify regions and centres of major activity where the coordinates of the introductions aggregated into groups. Thus, for each period identified with the multiobjective optimization, the cluster analysis grouped the introduction coordinates of Figure 1a based on their vicinity. In particular, we used a cluster approach developed for community detection in association networks implemented in *igraph* (Csardi & Nepusz, 2006) to identify centres during each period obtained with the multiobjective optimization. Based exclusively on the coordinates of the introductions that took place in each of these periods, we carried out a global triangulation, using the function *convhulln* implemented in the *R* package *geometry* (Habel et al., 2019). Then, we derived the connections and weights (i.e., distances between connected coordinates) to build one network per period from each triangulation. The resulting networks were simplified by removing distant connections (Rozenfeld et al., 2008) and the function *cluster_edge_betweenness* (Newman & Girvan, 2004) was used to identify the major introduction centres. Subsequently, origin and species of the clustered introductions was studied. The donor biogeographic regions of the species involved in each cluster were then depicted as pie charts centred at the mean coordinates of the introduction centre to visualize global spatial introduction patterns within each period. An analogous figure depicting the most frequently introduced species in each period is provided in Supplementary material S1 (Figure S11).

Temporal trends in species introduction distances

To calculate the distance between known donor and recipient sites, we used the haversine formula (Figure S2 in Supplementary material S1). Then, we used violin plots, as implemented in the *R* package *vioplot* (Adler & Kelly, 2020), and PERMANOVA, respectively, to visualize and test for temporal changes in these distances between the periods identified with the multiobjective optimization. The PERMANOVA was carried out using the function *adonis* (*permutations* = 9999), and the complementary test to confirm the homogeneous dispersion of the groups was done using *betadisper*, both from the package *vegan*.

3 | RESULTS

The Palearctic region experienced the largest number of introduction events (1502), including repeated introductions of a given species (Figure 2). This region was followed by the Sino-Oriental region (1020), whereas the Madagascan region only received 106 introductions. The most important donor was the Sino-Oriental region, which had species involved in 1195 introductions. By contrast, only four introductions involved species originating from the Madagascan region, as only one single species (*Pachypanchax playfairii*) was endemic to this region. The largest species flow corresponded to species native to the Palearctic region (590), followed by introductions of species native to the Sino-Oriental region (431). By contrast, Madagascan species have been introduced solely in the Palearctic and Sino-Oriental regions (see Figure S6 in Supplementary material S1 for further information considering only first records).

The frequencies of the different species introduced varied markedly among biogeographic regions ($\chi^2 = 6272.5$, $df = 4122$, $p < 0.001$). The largest proportions of species introduced only once occurred in the Madagascan region (93.3%) and the lowest in the Ethiopian region (36.0%) (Figure 3a). Among the 268 species introduced in two or more regions (39.0%), 23 species were introduced in every biogeographic region (3.3%). The Madagascan and Palearctic regions had the largest dissimilarity in introduced species composition, whereas the Ethiopian and Neotropical regions had

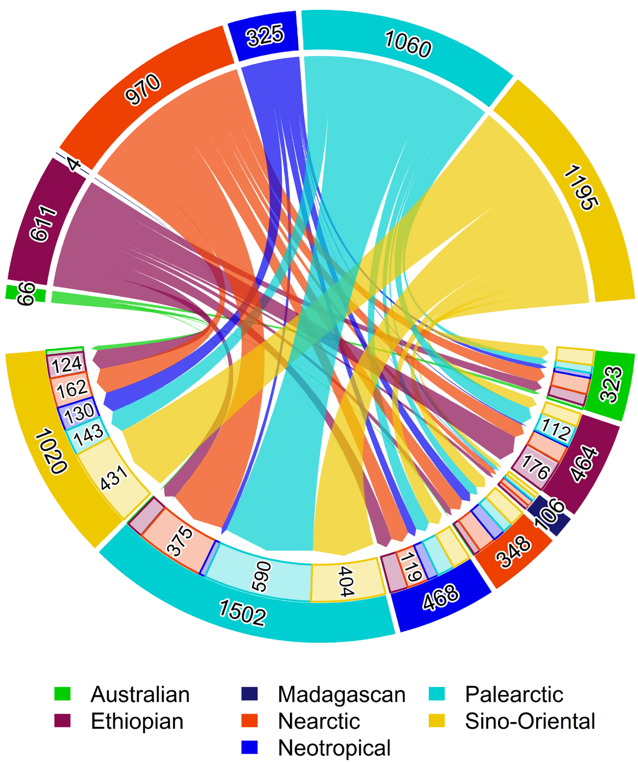

FIGURE 2 Flow diagrams of the total number of freshwater fish introduction events ($n = 4233$). The numbers indicate the total number of events, including repeated introductions. An analogous figure for the number of species introduced can be found in Supplementary material S1 (Figure S6).

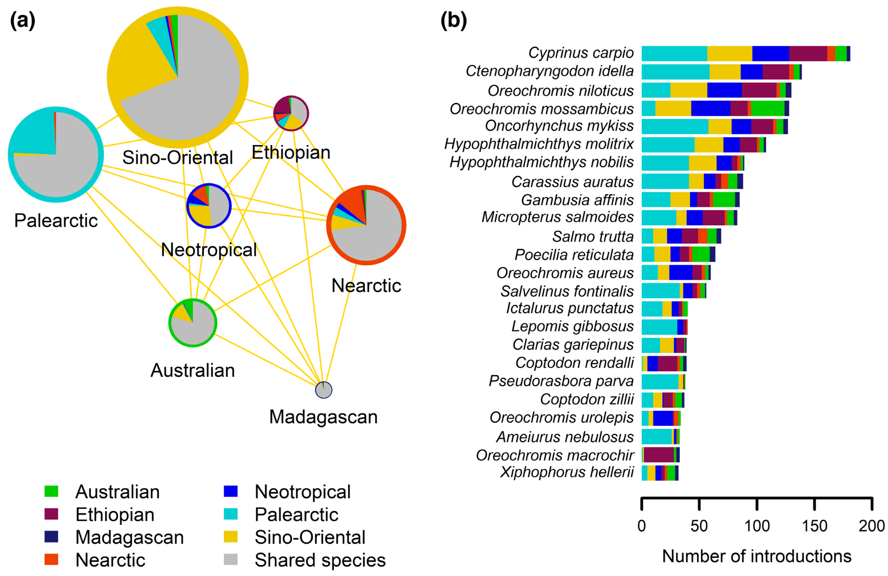

FIGURE 3 (a) Undirected graph based on the Bray–Curtis dissimilarity between the total number of introductions per species and biogeographic region. Edge length is proportional to the inverse distance between regions (1–Bray–Curtis dissimilarity). Pie charts depict the per cent of shared species (grey) and exclusive species (i.e., introduced in one single biogeographic region). The origin of the exclusive species has been split by biogeographic region of origin. Pie chart sizes are proportional to the total number of introduction events. (b) Barplot of the 24 most frequently introduced species (41.9% of all known introduction events) by recipient biogeographic region.

the smallest. Species shared among two or more biogeographic regions dominated every biogeographic region, except the Ethiopian and Neotropical ones (Figure 3a grey sectors). The species introduced solely in the Palearctic, Sino-Oriental or Ethiopian regions corresponded mostly to intraregional introductions, although in the Ethiopian and Neotropical regions Sino-Oriental species introductions were frequent. In the remaining regions, they corresponded to species that originated in distinct freshwater fish regions.

The most widely introduced species was the common carp (*C. carpio*, 181 introductions), followed by other cypriniformes (*Ctenopharyngodon idella*, *Hypophthalmichthys molitrix*, *Hypophthalmichthys nobilis* and *Carassius auratus*), cichlids including tilapias (*Oreochromis niloticus*, *Oreochromis mossambicus* and *Oreochromis aureus*), salmonids (*Oncorhynchus mykiss*), poeciliids (*Gambusia affinis*) and centrarchids (*Micropterus salmoides*; Figure 3b). Taken together, the ten most widely introduced species accounted for 27.7% of all reported introduction events, whereas the 24 species depicted in Figure 3b account for 41.9% of all known introductions (Supplementary material S2 shows the complete list of introductions per species and biogeographic region). Salmonid and cypriniform introductions dominate the Palearctic region, whereas cultured cichlids (mainly tilapias—*Oreochromis* spp.) have been frequently introduced in the Sino-Oriental region, and they dominated in the Ethiopian and Neotropical regions.

We identified three plausible breakpoints in temporal dynamics of introductions, located at years 1862, 1947 and 1995 (see section 3.2 in Supplementary material S1 for further information about the results of the multiobjective optimization).

The species and frequency of introductions depended on the recipient biogeographic regions, and this relationship varied with time (PERMANOVA tests, $p < 0.005$). The introductions in the Palearctic region with known date outnumbered those in the other regions during the four periods, although after 1947 the number of introductions approximated those occurring in the Sino-Oriental region, which were more frequent towards the end of the century (Figure 4a). The frequency of reported introductions in the Sino-Oriental, Ethiopian and Neotropical regions has increased across periods, but those in the Nearctic Australian and Madagascan regions have remained mostly constant across time. The reported introductions markedly declined during World War I (WWI) and World War II (WWII).

Salmonid and cypriniform introductions spanned the four periods identified (Figure 4b). By contrast, cichlids, including tilapias (e.g., *Oreochromis* spp.), and catfish introductions (e.g., *Ictalurus punctatus* and *Clarias gariepinus*), both related to aquaculture, have been more common during the latter periods, although the introduction of salmonids and tilapias extended into the last period after 1995. The peak of introductions of *G. affinis* (a poeciliid introduced for mosquito control programmes) occurred during the interwar period. The violin plots also illustrate the reduction in the number of introductions during WWI and WWII for some species (e.g., *Salvelinus fontinalis*, *Tinca tinca*, *O. mykiss* or *M. dolomieu*) and the considerable replacement of species over time.

The cluster analysis supported the results of the PERMANOVA indicating the existence of several, yet temporally changing, centres receiving introduced species from different donor regions in each period. Most species introduced between 1800 and 1862 (38 introductions) originated from the Palearctic and Sino-Oriental regions and were principally cypriniformes (see Figure 5 and Figure S11 in Supplementary material S1 for information on the specific introduced species). Introductions were evenly distributed across

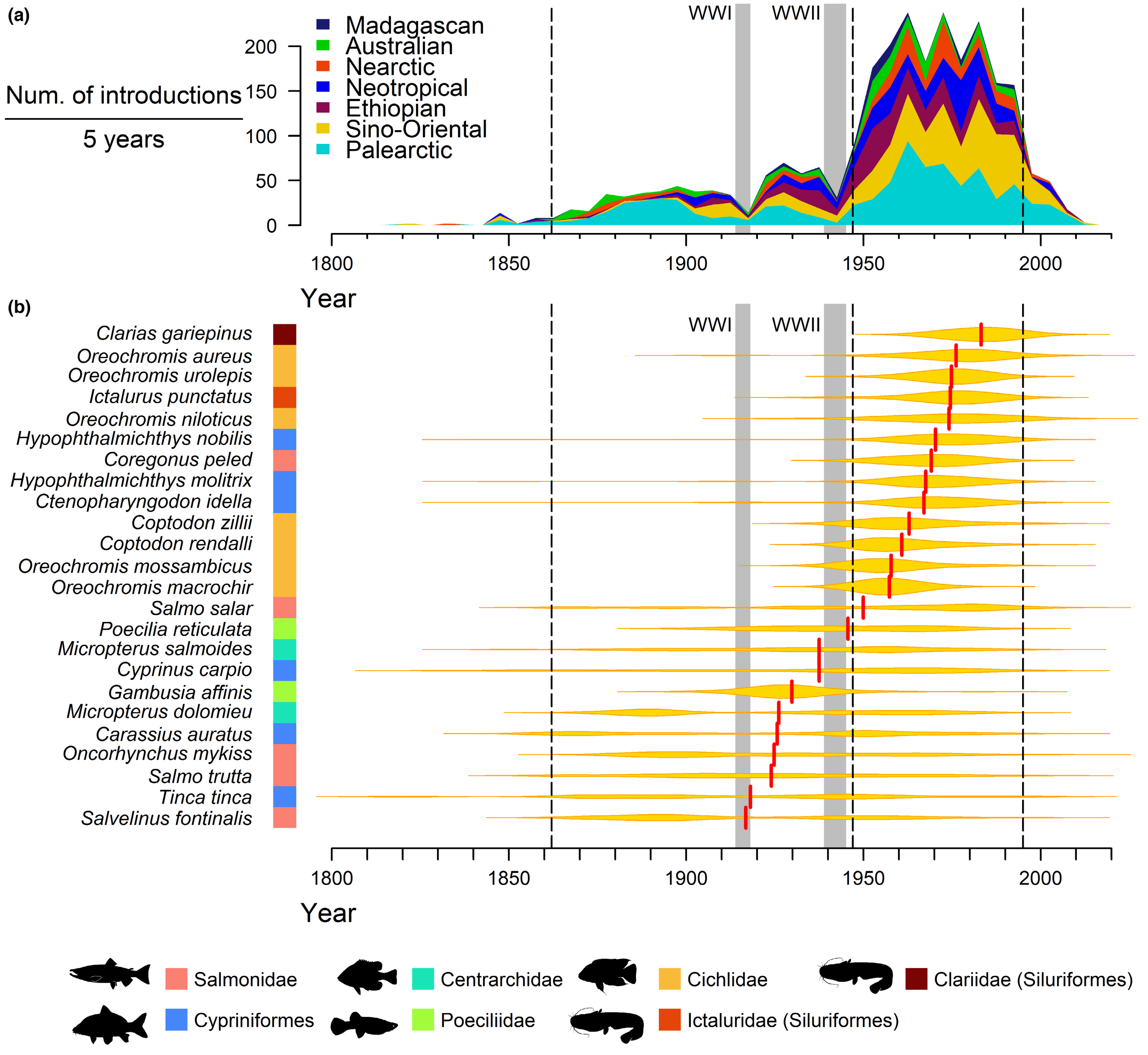

FIGURE 4 (a) Number of introductions per five-year period and biogeographic region. The reported introductions markedly diminished during World War I (WWI) and World War II (WWII) (grey strips). Dashed grey lines indicate the breakpoints of the four distinct introduction periods with homogeneous introduction rates and introduced species (see Methods and Figures S8 and S9 for information on how these periods were identified). (b) Violin plots of the introduction dates of most introduced species with known introduction dates. The red segments depict the mean values. Grey strips indicate WWI and WWII and dashed grey lines the breakpoints of the four distinct introduction periods.

regions, although no introductions were reported in Asia, the Middle East and the north of the Neotropical region.

Between 1863 and 1947, the total number of introductions rose dramatically (649 introductions, +1608%) and was dominated by Nearctic species followed by Palearctic salmonids. Europe and the Middle East received the most introductions. The only exception to this general pattern was the introduction centre encompassing the Sino-Oriental and Australian regions, where substantial proportions corresponded to aquaculture (*Hypophthalmichthys* spp.) and ornamental (*C. auratus*) Sino-Oriental cypriniformes.

The third period (1943–1995) had the highest number of reported introduction events (i.e., 1836). The species origin changed considerably compared with former periods, and there was a broader inclusion of species from different freshwater fish biogeographic regions. Neotropical species were the most frequently introduced in North America; Ethiopian ones in Central and South America (mainly cultured cichlids), although Palearctic and Sino-Oriental species still encompassed a great proportion. In Europe and the Middle East, most of the introduced species came from the Palearctic or were aquaculture Sino-Oriental cypriniformes. Species of Ethiopian origin dominated

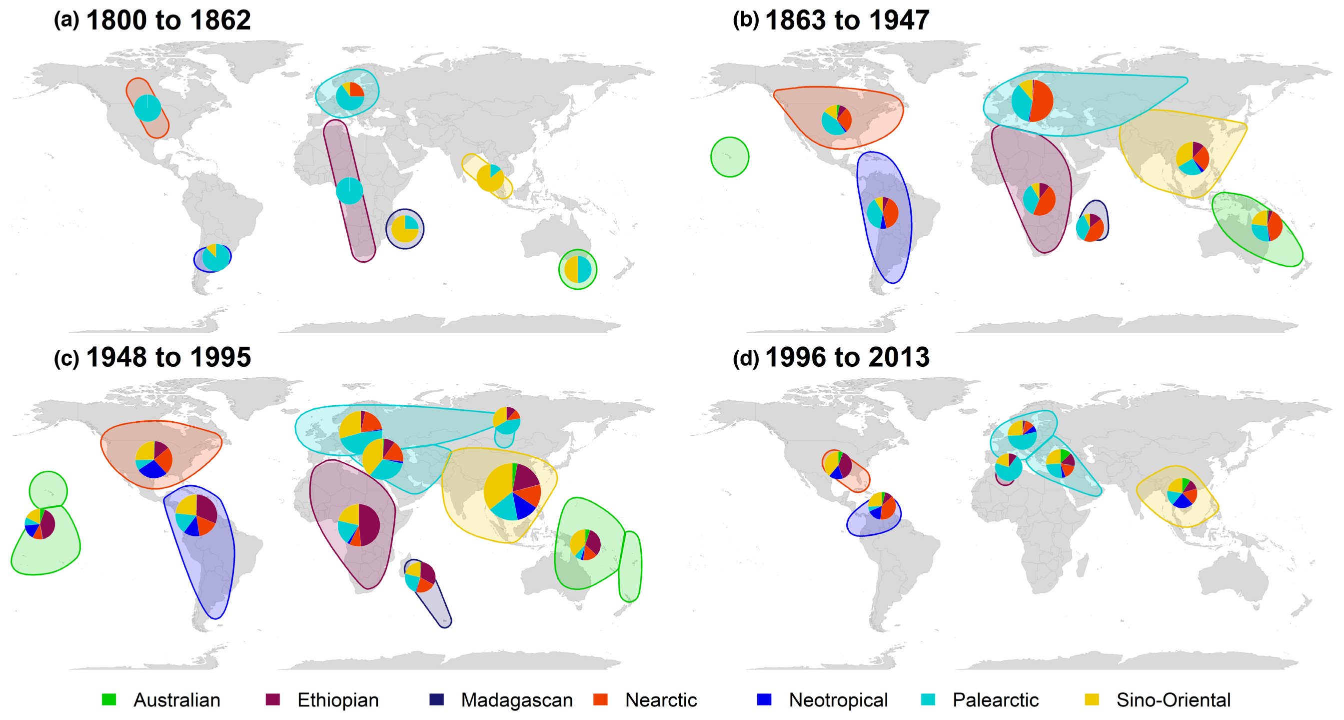

FIGURE 5 Introduction centres and origin of the introduced fish species for each period with homogeneous introduction rates and similar array of introduced species (see Methods and Figures S9 and S10 for information on how these periods were identified). The size of the pie charts is proportional to the log-transformed number of introduction events ($n_a = 38$, $n_b = 649$, $n_c = 1836$ and $n_d = 128$, introductions). Coloured areas encompass the coordinates of the locations clustered in each centre and pie chart. An analogous figure depicting the most frequently introduced species in each period can be found in Supplementary material S1 (Figure S11).

the African continent, whereas in the Sino-Oriental, Madagascan and Australian regions around the Indian Ocean the species origins were the most diverse, although cultured cichlids prevailed.

During the last period from 1996 to 2013, the species origin was the most diverse in every region compared with former periods, except in the Mediterranean, where Palearctic species predominated. The introductions of the most common species were infrequent in this period.

Mean distances between donor and recipient sites did not significantly vary among periods (PERMANOVA $p = 0.107$) but were less variable in the first period from 1800 to 1862 (beta dispersion $p = 0.04$; Figure 6). Median distances ranged between 3430 (third period) and 3977 km (second period), but shorter distances were overrepresented ($Mode_{distance} = 1729.5$ km). The minimum reported distance was 22.7 km and corresponded to the translocation of the Nile Tilapia (*O. niloticus*) between two nearby lakes, whereas introductions over more than 18,000 km have been reported in every period and were mostly introductions from Europe to New Zealand.

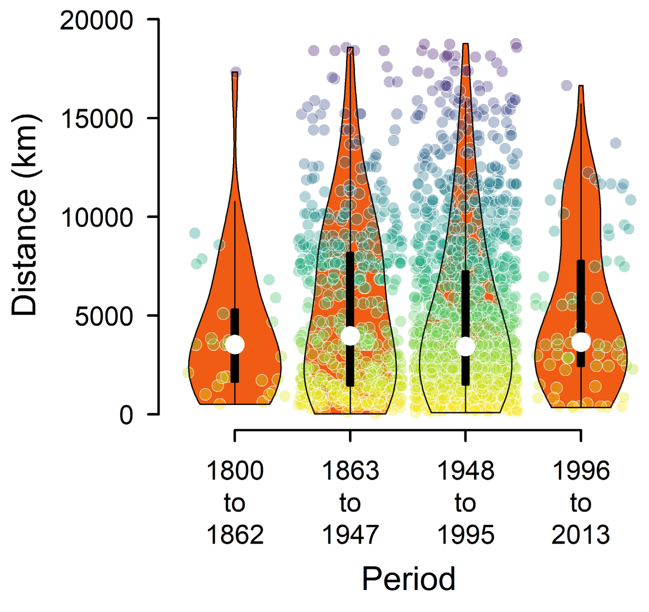

FIGURE 6 Violin plots of the distances between donor and recipient sites by period with homogeneous introduction rates and similar array of introduced species (see Methods and Figures S9 and S10 for information on how these periods were identified).

4 | DISCUSSION

We found evidence for substantial spatio-temporal changes in global freshwater fish introductions from 1800 onwards. Before 1862, introduction patterns among biogeographic regions, and introduced species, mirrored geopolitical and trading network developments, as indicated by the number of Nearctic fish species introduced to Europe, a phenomenon facilitated by the tight political and socio-economic links between Europe and North America (Chapman et al., 2017). The diaspora of European settlers, by contrast, spread Palearctic species all over the globe (Krull et al., 2014; Lenzner et al., 2018), whereas the popularity of aquaculture in Asia, and its proximity, contributed to the large number of Sino-Oriental introductions around the Indian Ocean before 1862 (Ahmed & Thompson, 2019; Garlock et al., 2020; Liu et al., 2018). Our results also highlight the popularity of mosquito control programmes for a short period after the 1920s (Gachelin et al., 2018) and, furthermore, reflected the increase in recreational fishing, pet keeping and aquaculture. The Nearctic region donated numerous species, especially from 1863 to 1947, when it dominated the flows of alien fishes. By contrast, the Ethiopian, Neotropical and, especially, the Sino-Oriental regions have emerged, or consolidated in the last case, as prominent global donor and recipient regions after WWII. During the last period (1996–2013), the analysis of the Fishbase dataset suggested a decrease in the number of introductions. However, considering recent studies highlighting the unexpected surge of certain fish species previously deemed to have low invasion potential (e.g., Clavero et al., 2023), it can be concluded that this finding most probably reflects a recording lag in Fishbase. Fishbase is one of the most comprehensive databases on fish introductions (Casal, 2006; Maldonado et al., 2015; Ruesink, 2005), but it has been shown that new records of alien species need several years to be comprehensively made available (Seebens et al., 2020).

The largest number of introductions corresponded to translocations within the Palearctic and within the Sino-Oriental regions, respectively, although the Palearctic region, in turn, received numerous introductions of Nearctic and Sino-Oriental species, often due to the similar climate of these three regions (Maceda-Veiga et al., 2013). Aquaculture has a long tradition in China and other Asian countries, which based on our results contributed to the comparatively high number of Sino-Oriental cypriniform introductions across the globe (e.g., *C. carpio*, *C. idella*, *H. molitrix* or *H. nobilis*) (Ahmed & Thompson, 2019; Garlock et al., 2020; Liu et al., 2018). Nonetheless, aquaculture already flourished between 2000 and 1000 BCE in ancient Egypt and Rome but especially in China, where it lasts until today (Ahmed & Thompson, 2019; Carpio et al., 2019). By contrast, aquaculture-related introductions in Europe have been of minor importance and only recently gained prominence (Balon, 1995; Mitchell, 2009). Nevertheless, European examples of aquaculture-related introductions exist, for example, the tench *T. tinca* (Clavero, 2019), which ranked 23rd among species in our analysis.

Contrary to Asia, where aquaculture-related introductions dominated, the introduction of recreational fish species in Europe contributed the most to the high number of reported introductions in this region, especially after WWII as revealed by the cluster analysis. Ornamental fishkeeping was, however, historically more popular in the Sino-Oriental region, which has led to a higher percentage of species introductions in this continent (Gozlan, 2008). Nonetheless, the goldfish (*C. auratus*) was domesticated with ornamental purposes in China around 1000 CE and currently occupies the 8th position in the group of most frequently introduced species. Due to limited access to natural spring water, it was not until the 17th century that these ornamentals were introduced in Europe, but they subsequently spread rapidly across western water bodies (Maceda-Veiga et al., 2019; Mitchell, 2009).

The Nearctic region proved to be a larger donor than recipient in every period, particularly towards the Palearctic region, for which Nearctic introductions outnumbered Palearctic introductions, even before 1862. This role as net donor was favoured by the large increase in traded live organisms as a consequence of the industrial revolution that facilitated the successful transport and subsequent spread of fish species over this climatically similar region (Seebens et al., 2019; Stevens et al., 2017). Nonetheless, the last period, although the lowest in terms of introduction events, was the most diverse in terms of origins. Cultured and sport fishes, especially salmonids (e.g., *O. mykiss* or *S. fontinalis*) and centrarchids (*Micropterus* spp.), have been introduced all over the studied period, while after WWII catfishes (*I. punctatus*) and poeciliids (e.g., *Poecilia reticulata*) emerged as prominent species among these transfers. This condition as net donor also reflects the great role played by local freshwater fish species, first for subsistence, and currently for recreation (Li et al., 2018), which comparatively disfavoured the introduction of alien fishes, despite the numerous introductions of foreign species that took place recently (Hughes, 2015). Conversely, the number of fishes donated by this region has most likely been favoured by the promotion carried out by aquarists during the last decades (Olden et al., 2021) and, especially by the high number of anglers residing in the USA (approx. 30 million people; Arlinghaus et al., 2015).

The historical importance of the Palearctic and Nearctic regions as donors has been previously highlighted (Lenzner et al., 2018; Su et al., 2020). However, several results indicate that the Sino-Oriental region is the most important donor and recipient region currently. Nonetheless, when we considered only the number of species introduced within each region, the ranking between the Palearctic and Sino-Oriental region was inverted (110 vs. 167 species; see Figure S6 in Supplementary material S1). This indicates that multiple introductions in the Palearctic region are likely secondary introductions that can be framed within a process of 'range filling' (Dominguez Almela et al., 2020). In addition, multiple pieces of evidence suggest that the ultimate number of different species and/or introductions in the Sino-Oriental region could outnumber that of the Palearctic because (i) the Sino-Oriental ichthyofauna is among the most diverse in the world, which may make species identification more difficult (Pimm et al., 2014), (ii) there is typically a bias in the compiled datasets that may lead to overestimating the importance of Europe and North America (Seebens et al., 2018), (iii) the Sino-Oriental region, particularly South East Asia, has a long tradition of aquaculture (Ahmed & Thompson, 2019), and (iv) it is currently a main exporter of ornamental fishes (Evers et al., 2019). These lines of reasoning are largely also applicable to the Ethiopian and Neotropical regions. Moreover, the number of Neotropical species introduced to the Sino-Oriental and Nearctic regions (75 and 50; see Figure S6) surpass those from the Palearctic, which highlights the increasing importance of the Neotropical region as a global donor. Nonetheless, this region is currently another hotspot in ornamental fish trade (Evers et al., 2019). Conversely, the relevance of the Ethiopian region is based on fewer species (it has donated 160 species) involved in numerous introductions (464 events). Therefore, it can be concluded that the Sino-Oriental region consolidated its prominence and the Ethiopian and Neotropical regions have emerged as new global donor and recipient regions of freshwater fish introductions as a reflection of new global introduction patterns and economic developments.

Freshwater fish introductions impact recipient ecosystems in multiple ways as they can increase predation, competition and hybridization, introduce new pathogens and modify food webs (Almeida & Grossman, 2012). Overall, these introductions have caused increasing homogenization of fish faunas all over the globe (Marr et al., 2013; Olden et al., 2018; Villéger et al., 2011). However, the impacts and ultimate consequences vary depending on the fish family. Large cypriniformes, such as the common and grass carps, tend to affect habitat quality due to their voracious appetite for aquatic flora, ultimately favouring the occurrence of algal blooms (Kloskowski, 2011; Zhao et al., 2020). By contrast, salmonid introductions tended to increase competition, displacing native individuals towards suboptimal habitats, eventually leading to species extirpations (Hasegawa, 2020), although its ability to establish and reproduce in recipient regions varied enormously (Koutsikos et al., 2019). Tilapias and catfishes exert multiple impacts in the recipient ecosystems as they have been linked to both species' extirpations and eutrophication processes (Weyl et al., 2016). This variety of outcomes led some scientist to label the ultimate consequences of freshwater fish introductions as the 'Frankenstein effect' due to the unpredictable developments of alien fish introductions on native fauna and ecosystems (Elvira & Almodóvar, 2001; Moyle et al., 1986). Nonetheless, the successful establishment of introduced fish strongly depends on the species' traits and their interaction with the different biotic and abiotic element of recipient ecosystems (García-Berthou, 2007).

Given these uncertainties, it becomes clear that newly emerging alien fish species should be the subject of future horizon scanning studies, aiming at identifying door-knocker species (i.e., species of high risk of arrival, establishment and impact; Seebens et al., 2018), and close precautionary monitoring, especially in a context of global warming that may facilitate the naturalization of warm-water species (Rahel & Olden, 2008). The most concerning species of this group might be the cichlids, including tilapias (e.g., *Oreochromis* spp.), and catfishes (e.g., *I. punctatus* and *C. gariepinus*) used in aquaculture, because they encompass the most recent and frequent introductions recorded in FishBase. Nonetheless, their ranges may increase globally as global warming facilitates their acclimatization in aquaculture facilities, although any fish species can likewise become established (Clavero et al., 2023).

Long-distance transcontinental introductions such as those involving Palearctic species brought by Europeans to temperate colonies (e.g., New Zealand) have been frequent all over the studied period and may be favoured in future by new trading routes like the Belt and Road Initiative connecting China and Europe (Bernery et al., 2022). However, the bulk of introductions involved distances between donor and recipient regions not exceeding 2000 km, probably due to the difficulties of transporting live fishes inexpensively (Stevens et al., 2017). This variability in the distances between donor and recipient regions highlights the difficult ranking of current threats, as species with distant native ranges can also be introduced (Chapman et al., 2017; Seebens et al., 2018). Anyhow, releases and escapes (sensu Hulme et al., 2008) are the main introduction pathways of freshwater fish species (Muñoz-Mas & García-Berthou, 2020), which indicates that sport fishers should be targeted in awareness-raising campaigns jointly with aquaculturists and aquarists, due to the recent increment in online trade (Bernery et al., 2022; Olden et al., 2021), to promote best practices and impede the spread of these species in natural environments.

During the last 100 years, national and international campaigns and legislation addressed to prevent alien species introductions and subsequent establishment have gained importance (Maceda-Veiga et al., 2019; McGeoch et al., 2010). However, still thousands of additional introductions of alien species took place (Seebens et al., 2017), which is reflected in the variety of newly introduced species (Figure S11 in Supplementary material S1) and origin observed during the most recent discriminated period (1996–2013). Range filling and expansion are often still ongoing for already introduced fish species. As a consequence, many more alien fish introductions can be expected. Global policy should thus pay special attention to tropical ornamental and aquaculture species, which could benefit from global warming and the rise of aquaculture to meet the increasing demands for animal protein, especially in the Sino-Oriental, Ethiopian and Neotropical regions. The Sino-Oriental region consolidated its predominance and the Ethiopian and Neotropical regions emerged in recent decades as major global donor and recipient regions, with important implications for potential impacts, management and monitoring after WWII. Enhancing knowledge about the historical development and current trends of alien fish introductions is essential for prioritizing monitoring programmes and tailoring preventive measures (Chapman et al., 2017).

ACKNOWLEDGEMENTS

We are indebted to the many people who contributed to the data on fish introductions used in this study and Dr. Boris Leroy and an anonymous reviewer for helpful comments on the manuscript. Open Access funding provided thanks to the CRUE-CSIC agreement with John Wiley & Sons, Inc.

FUNDING INFORMATION

This research is part of projects CGL2016-80820-R, RED2018-102571-T and PID2019-103936GB-C21 and TED2021-129889B-I00 financially supported by MCIN/AEI/10.13039/501100011033. Additional financial support was provided by the sTWIST working group (Theory and Workflows for Invasive Species Tracking) supported by sDiv, the Synthesis Centre of iDiv (DFG FZT 118 – 202548816). RMM benefitted from a postdoctoral Juan de la Cierva fellowship from the Spanish Ministry of Science (ref. FJCI-2016-30,829). FE and HS received funding through the 2017–2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND programme, and with the funding organization FWF ('AlienScenarios', project no I 4011-B32) and BMBF ('AlienScenarios' 16LC1807A).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data used in this research are available at doi: 10.6084/m9.figshare.19563193.v1.

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REFERENCES

Adler, D., & Kelly, S. T. (2020). vioplot: Violin plot. https://github.com/TomKellyGenetics/vioplot

Ahmed, N., & Thompson, S. (2019). The blue dimensions of aquaculture: A global synthesis. *Science of the Total Environment*, *652*, 851–861. https://doi.org/10.1016/j.scitotenv.2018.10.163

Almeida, D., & Grossman, G. D. (2012). Utility of direct observational methods for assessing competitive interactions between non-native and native freshwater fishes. *Fisheries Management and Ecology*, *19*(2), 157–166. https://doi.org/10.1111/j.1365-2400.2012.00847.x

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46. https://doi.org/10.1046/j.1442-9993.2001.01070.x

Arbelaitz, O., Gurrutxaga, I., Muguerza, J., Pérez, J. M., & Perona, I. (2013). An extensive comparative study of cluster validity indices. *Pattern Recognition*, *46*(1), 243–256. https://doi.org/10.1016/j.patcog.2012.07.021

Arlinghaus, R., Tillner, R., & Bork, M. (2015). Explaining participation rates in recreational fishing across industrialised countries. *Fisheries Management and Ecology*, *22*(1), 45–55. https://doi.org/10.1111/fme.12075

Balon, E. K. (1995). Origin and domestication of the wild carp, *Cyprinus carpio*: From Roman gourmets to the swimming flowers. *Aquaculture*, *129*(1), 3–48. https://doi.org/10.1016/0044-8486(94)00227-F

Bernery, C., Bellard, C., Courchamp, F., Brosse, S., Gozlan, R., Jarić, I., Teletchea, F., & Leroy, B. (2022). Freshwater fish invasions: A comprehensive review. *Annual Review of Ecology, Evolution, and Systematics*, *53*, 427–456. https://doi.org/10.1146/annurev-ecolsys-032522-015551

Capinha, C., Essl, F., Seebens, H., Moser, D., & Pereira, H. M. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, *348*(6240), 1248–1251. https://doi.org/10.1126/science.aaa8913

Carpio, A. J., De Miguel, R. J., Oteros, J., Hillström, L., & Tortosa, F. S. (2019). Angling as a source of non-native freshwater fish: A European review. *Biological Invasions*, *21*(11), 3233–3248. https://doi.org/10.1007/s10530-019-02042-5

Casal, C. M. V. (2006). Global documentation of fish introductions: The growing crisis and recommendations for action. *Biological Invasions*, *8*(1), 3–11. https://doi.org/10.1007/s10530-005-0231-3

Chan, F. T., Beatty, S. J., Jr., Giles, A., Hill, J. E., Luo, D., Morgan, D. L., Pavia, R. T. B., Jr., Therriault, T. W., Verreycken, H., Vilizzi, L., Wei, H., Yeo, D. C. J., Zeng, Y., Zięba, G., & Copp, G. H. (2020). Leaving the fish bowl: The ornamental trade as a global vector for freshwater fish invasions. *Aquatic Ecosystem Health & Management*, *22*(4), 417–439. https://doi.org/10.1080/14634988.2019.1685849

Chapman, D., Purse, B. V., Roy, H. E., & Bullock, J. M. (2017). Global trade networks determine the distribution of invasive non-native species. *Global Ecology and Biogeography*, *26*(8), 907–917. https://doi.org/10.1111/geb.12599

Clavero, M. (2019). Beyond one bone: Interdisciplinarity to assess nativeness of the tench (*Tinca tinca*) in Spain. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(11), 1863–1869. https://doi.org/10.1002/aqc.3184

Clavero, M., Suh, J., Franch, N., Aparicio, E., Buchaca, T., Caner, J., Garcia-Rodriguez, S., Llimona, F., Pou-Rovira, Q., Rocaspana, R., & Ventura, M. (2023). Invaders they are a-changing†: A recent, unexpected surge of invasive loaches in Catalonia. *Freshwater Biology*, *68*, 621–631. https://doi.org/10.1111/fwb.14051

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Systems*, *1695*(5), 1–9.

Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T. M., Dyer, E. E., Cassey, P., Scrivens, S. L., Economo, E. P., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., … Essl, F. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology & Evolution*, *1*(7), 0186. https://doi.org/10.1038/s41559-017-0186

Deb, K., Pratap, A., Agarwal, S., & Meyarivan, T. (2002). A fast and elitist multiobjective genetic algorithm: NSGA-II. *IEEE Transactions on Evolutionary Computation*, *6*(2), 182–197. https://doi.org/10.1109/4235.996017

Dias, M. S., Oberdorff, T., Hugueny, B., Leprieur, F., Jézéquel, C., Cornu, J. F., Brosse, S., Grenouillet, G., & Tedesco, P. A. (2014). Global imprint of historical connectivity on freshwater fish biodiversity. *Ecology Letters*, *17*(9), 1130–1140. https://doi.org/10.1111/ele.12319

Dominguez Almela, V., Palmer, S. C. F., Gillingham, P. K., Travis, J. M. J., & Britton, J. R. (2020). Integrating an individual-based model with approximate Bayesian computation to predict the invasion of a freshwater fish provides insights into dispersal and range expansion dynamics. *Biological Invasions*, *22*, 1461–1480. https://doi.org/10.1007/s10530-020-02197-6

Ellender, B. R., Woodford, D. J., Weyl, O. L. F., & Cowx, I. G. (2014). Managing conflicts arising from fisheries enhancements based on non-native fishes in southern Africa. *Journal of Fish Biology*, *85*(6), 1890–1906. https://doi.org/10.1111/jfb.12512

Elvira, B., & Almodóvar, A. (2001). Freshwater fish introductions in Spain: Facts and figures at the beginning of the 21st century. *Journal of Fish Biology*, *59*, 323–331. https://doi.org/10.1006/jfbi.2001.1753

Epskamp, S., Cramer, A. O. J., Waldorp, L. J., Schmittmann, V. D., & Borsboom, D. (2012). Qgraph: Network visualizations of relationships in psychometric data. *Journal of Statistical Software*, *48*(4), 1–18. https://doi.org/10.18637/jss.v048.i04

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Pyšek, P., Wilson, J. R. U., & Richardson, D. M. (2015). Historical legacies accumulate to shape future biodiversity in an era of rapid global change. *Diversity and Distributions*, *21*(5), 534–547. https://doi.org/10.1111/ddi.12312

Evers, H., Pinnegar, J. K., & Taylor, M. I. (2019). Where are they all from? – Sources and sustainability in the ornamental freshwater fish trade. *Journal of Fish Biology*, *94*(6), 909–916. https://doi.org/10.1111/jfb.13930

Froese, R., & Pauly, D. (2022). FishBase. Retrieved February 1, 2021, from World Wide Web electronic publication. www.fishbase.org

Fruchterman, T. M. J., & Reingold, E. M. (1991). Graph drawing by force-directed placement. *Software: Practice and Experience*, *21*(11), 1129–1164. https://doi.org/10.1002/spe.4380211102

Gachelin, G., Garner, P., Ferroni, E., Verhave, J. P., & Opinel, A. (2018). Evidence and strategies for malaria prevention and control: A historical analysis. *Malaria Journal*, *17*(1), 96. https://doi.org/10.1186/s12936-018-2244-2

García-Berthou, E. (2007). The characteristics of invasive fishes: What has been learned so far? *Journal of Fish Biology*, *71*, 33–55. https://doi.org/10.1111/j.1095-8649.2007.01668.x

Garlock, T., Asche, F., Anderson, J., Bjørndal, T., Kumar, G., Lorenzen, K., Ropicki, A., Smith, M. D., & Tveterås, R. (2020). A global blue revolution: Aquaculture growth across regions, species, and countries.

Reviews in Fisheries Science and Aquaculture, 28(1), 107–116. https://doi.org/10.1080/23308249.2019.1678111

Gozlan, R. E. (2008). Introduction of non-native freshwater fish: Is it all bad? *Fish and Fisheries*, *9*(1), 106–115. https://doi.org/10.1111/j.1467-2979.2007.00267.x

Gu, Z., Gu, L., Eils, R., Schlesner, M., & Brors, B. (2014). *Circlize* implements and enhances circular visualization in R. *Bioinformatics*, *30*(19), 2811–2812. https://doi.org/10.1093/bioinformatics/btu393

Gunantara, N. (2018). A review of multi-objective optimization: Methods and its applications. *Cogent Engineering*, *5*(1), 1502242. https://doi.org/10.1080/23311916.2018.1502242

Habel, K., Grasman, R., Gramacy, R. B., Mozharovskyi, P., & Sterratt, D. C. (2019). *geometry: mesh generation and surface tessellation*.

Hasegawa, K. (2020). Invasions of rainbow trout and brown trout in Japan: A comparison of invasiveness and impact on native species. *Ecology of Freshwater Fish*, *29*(3), 419–428. https://doi.org/10.1111/eff.12534

Haubrock, P. J., Bernery, C., Cuthbert, R. N., Liu, C., Kourantidou, M., Leroy, B., Turbelin, A. J., Kramer, A. M., Verbrugge, L. N. H., Diagne, C., Courchamp, F., & Gozlan, R. E. (2022). Knowledge gaps in economic costs of invasive alien fish worldwide. *Science of the Total Environment*, *803*, 149875. https://doi.org/10.1016/j.scitotenv.2021.149875

Hughes, R. M. (2015). Recreational fisheries in the USA: Economics, management strategies, and ecological threats. *Fisheries Science*, *81*(1), 1–9. https://doi.org/10.1007/s12562-014-0815-x

Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pyšek, P., Roques, A., Sol, D., Solarz, W., & Vilà, M. (2008). Grasping at the routes of biological invasions: A framework for integrating pathways into policy. *Journal of Applied Ecology*, *45*(2), 403–414. https://doi.org/10.1111/j.1365-2664.2007.01442.x

Kloskowski, J. (2011). Impact of common carp Cyprinus carpio on aquatic communities: Direct trophic effects versus habitat deterioration. *Fundamental and Applied Limnology*, *178*(3), 245–255. https://doi.org/10.1127/1863-9135/2011/0178-0245

Koutsikos, N., Vardakas, L., Zogaris, S., Perdikaris, C., Kalantzi, O.-I., & Economou, A. N. (2019). Does rainbow trout justify its high rank among alien invasive species? Insights from a nationwide survey in Greece. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(3), 409–423. https://doi.org/10.1002/aqc.3025

Krull, C. R., Galbraith, J. A., Glen, A. S., & Nathan, H. W. (2014). Invasive vertebrates in Australia and New Zealand. In A. Stow, N. Maclean, & G. I. Holwell (Eds.), *Austral ark: The state of wildlife in Australia and New Zealand* (pp. 197–226). Cambridge University Press. https://doi.org/10.1017/CBO9781139519960.012

Lenzner, B., Essl, F., & Seebens, H. (2018). The changing role of Europe in past and future alien species displacement. In R. Rozzi, R. H. May, Jr., F. S. Chapin, III, F. Massardo, M. C. Gavin, I. J. Klaver, A. Pauchard, M. A. Nuñez, & D. Simberloff (Eds.), *From biocultural homogenization to biocultural conservation* (pp. 125–135). Springer International Publishing. https://doi.org/10.1007/978-3-319-99513-7_8

Leroy, B., Dias, M. S., Giraud, E., Hugueny, B., Jézéquel, C., Leprieur, F., Oberdorff, T., & Tedesco, P. A. (2019). Global biogeographical regions of freshwater fish species. *Journal of Biogeography*, *46*(11), 2407–2419. https://doi.org/10.1111/jbi.13674

Leuven, R. S. E. W., van der Velde, G., Baijens, I., Snijders, J., van der Zwart, C., Lenders, H. J. R., & bij de Vaate, A. (2009). The river Rhine: A global highway for dispersal of aquatic invasive species. *Biological Invasions*, *11*(9), 1989–2008. https://doi.org/10.1007/s10530-009-9491-7

Li, D., Lockwood, J. L., & Baiser, B. (2018). Taxonomic and phylogenetic homogenization across US national parks: The role of non-native species. In R. Rozzi, R. H. May, Jr., F. S. Chapin, III, F. Massardo, M. C. Gavin, I. J. Klaver, A. Pauchard, M. A. Nuñez, & D. Simberloff (Eds.), *From biocultural homogenization to biocultural conservation* (pp. 275–288). Springer International Publishing. https://doi.org/10.1007/978-3-319-99513-7_17

Liu, J., Wang, Q., Yuan, J., Zhang, T., Ye, S., Li, W., Li, Z., & Gui, J.-F. (2018). Integrated rice-field aquaculture in China, a long-standing practice, with recent leapfrog developments. In J.-F. Gui, Q. Tang, Z. Li, J. Liu, & S. S. De Silva (Eds.), *Aquaculture in China* (pp. 174–184). John Wiley & Sons Ltd. https://doi.org/10.1002/9781119120759.ch2_6

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). *100 of the world's worst invasive alien species: A selection from the global invasive species database* (Vol. *12*). Invasive Species Specialist Group Auckland.

Ma, X., Bangxi, X., Yin-dong, W., & Mingxue, W. (2003). Intentionally introduced and transferred fishes in China's inland waters. *Asian Fisheries Science*, *16*, 279–290. https://doi.org/10.33997/j.afs.2003.16.4.001

Maceda-Veiga, A., Escribano, J., Martinez Silvestre, A., Verdaguer, I., & Mac Nally, R. (2019). What's next? The release of exotic pets continues virtually unabated seven years after enforcement of new legislation for managing invasive species. *Biological Invasions*, *21*(9), 2933–2947. https://doi.org/10.1007/s10530-019-02023-8

Maceda-Veiga, A., Escribano-Alacid, J., de Sostoa, A., & García-Berthou, E. (2013). The aquarium trade as a potential source of fish introductions in southwestern Europe. *Biological Invasions*, *15*(12), 2707–2716. https://doi.org/10.1007/s10530-013-0485-0

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2022). *Cluster: Cluster analysis basics and extensions*. https://CRAN.R-project.org/package=cluster

Maldonado, C., Molina, C. I., Zizka, A., Persson, C., Taylor, C. M., Albán, J., Chilquillo, E., Rønsted, N., & Antonelli, A. (2015). Estimating species diversity and distribution in the era of Big Data: To what extent can we trust public databases? *Global Ecology and Biogeography*, *24*(8), 973–984. https://doi.org/10.1111/geb.12326

Marr, S. M., Olden, J. D., Leprieur, F., Arismendi, I., Ćaleta, M., Morgan, D. L., Nocita, A., Šanda, R., Tarkan, A. S., & García-Berthou, E. (2013). A global assessment of freshwater fish introductions in mediterranean-climate regions. *Hydrobiologia*, *719*(1), 317–329. https://doi.org/10.1007/s10750-013-1486-9

McGeoch, M. A., Butchart, S. H. M., Spear, D., Marais, E., Kleynhans, E. J., Symes, A., Chanson, J., & Hoffmann, M. (2010). Global indicators of biological invasion: Species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, *16*(1), 95–108. https://doi.org/10.1111/j.1472-4642.2009.00633.x

McIntosh, A. R., McHugh, P. A., & Budy, P. (2011). Brown trout (*Salmo trutta*). In R. A. Francis (Ed.), *A handbook of global freshwater invasive species* (pp. 285–296). Earthscan.

Mitchell, M. A. (2009). History of exotic pets. In M. A. Mitchell & T. N. Tully (Eds.), *Manual of exotic pet practice* (pp. 1–3). W.B. Saunders. https://doi.org/10.1016/B978-141600119-5.50004-4

Moyle, P. B., Li, H. W., & Barton, B. A. (1986). The Frankenstein effect: Impact of introduced fishes on native fishes in North America. In R. H. Stroud (Ed.), *Fish culture in fisheries management* (pp. 415–426). American Fisheries Society.

Muggeo, V. M. R. (2003). Estimating regression models with unknown break-points. *Statistics in Medicine*, *22*(19), 3055–3071. https://doi.org/10.1002/sim.1545

Muggeo, V. M. R. (2008). Segmented: An R package to fit regression models with broken-line relationships. *R News*, *8*(1), 20–25.

Muñoz-Mas, R., & García-Berthou, E. (2020). Alien animal introductions in Iberian inland waters: An update and analysis. *Science of the Total Environment*, *703*, 134505. https://doi.org/10.1016/j.scitotenv.2019.134505

Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E – Statistical, Nonlinear, and Soft Matter Physics*, *69*(2), 026113. https://doi.org/10.1103/PhysRevE.69.026113

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szöcs, E., & Wagner, H. (2019). *Vegan: Community ecology package*.

Olden, J. D., Comte, L., & Giam, X. (2018). The Homogocene: A research prospectus for the study of biotic homogenisation. *NeoBiota*, *37*, 23–36. https://doi.org/10.3897/neobiota.37.22552

Olden, J. D., Whattam, E., & Wood, S. A. (2021). Online auction marketplaces as a global pathway for aquatic invasive species. *Hydrobiologia*, *848*, 1967–1979. https://doi.org/10.1007/s10750-020-04407-7

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/10.1126/science.1246752

R Development Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, *22*(3), 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*(3), 849–873. https://doi.org/10.1111/brv.12480

Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*, *20*, 53–65. https://doi.org/10.1016/0377-0427(87)90125-7

Rozenfeld, A. F., Arnaud-Haond, S., Hernández-García, E., Eguíluz, V. M., Serrão, E. A., & Duarte, C. M. (2008). Network analysis identifies weak and strong links in a metapopulation system. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(48), 18824–18829. https://doi.org/10.1073/pnas.0805571105

Ruesink, J. L. (2005). Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology*, *19*(6), 1883–1893. https://doi.org/10.1111/j.1523-1739.2005.00267.x-i1

Seebens, H. (2019). Invasion ecology: Expanding trade and the dispersal of alien species. *Current Biology*, *29*(4), R120–R122. https://doi.org/10.1016/j.cub.2018.12.047

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., van Kleunen, M., Winter, M., Ansong, M., Arianoutsou, M., Bacher, S., Blasius, B., Brockerhoff, E. G., Brundu, G., Capinha, C., Causton, C. E., Celesti-Grapow, L., … Essl, F. (2018). Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences*, *115*(10), E2264–E2273. https://doi.org/10.1073/pnas.1719429115

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*(14435), 1–9. https://doi.org/10.1038/ncomms14435

Seebens, H., Briski, E., Ghabooli, S., Shiganova, T., MacIsaac, H. J., & Blasius, B. (2019). Non-native species spread in a complex network: The interaction of global transport and local population dynamics determines invasion success. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1901), 20190036. https://doi.org/10.1098/rspb.2019.0036

Seebens, H., Clarke, D. A., Groom, Q., Wilson, J. R. U., García-Berthou, E., Kühn, I., Roigé, M., Pagad, S., Essl, F., Vicente, J., Winter, M., & McGeoch, M. (2020). A workflow for standardising and integrating alien species distribution data. *NeoBiota*, *59*, 39–59. https://doi.org/10.3897/neobiota.59.53578

Stevens, C. H., Croft, D. P., Paull, G. C., & Tyler, C. R. (2017). Stress and welfare in ornamental fishes: What can be learned from aquaculture? *Journal of Fish Biology*, *91*(2), 409–428. https://doi.org/10.1111/jfb.13377

Su, G., Villéger, S., & Brosse, S. (2020). Morphological sorting of introduced freshwater fish species within and between donor realms. *Global Ecology and Biogeography*, *29*(5), 803–813. https://doi.org/10.1111/geb.13054

Tedesco, P. A., Beauchard, O., Bigorne, R., Blanchet, S., Buisson, L., Conti, L., Cornu, J. F., Dias, M. S., Grenouillet, G., Hugueny, B., Jézéquel, C., Leprieur, F., Brosse, S., & Oberdorff, T. (2017). Data descriptor: A global database on freshwater fish species occurrence in drainage basins. *Scientific Data*, *4*(1), 1–6. https://doi.org/10.1038/sdata.2017.141

Toussaint, A., Beauchard, O., Oberdorff, T., Brosse, S., & Villéger, S. (2014). Historical assemblage distinctiveness and the introduction of widespread non-native species explain worldwide changes in freshwater fish taxonomic dissimilarity. *Global Ecology and Biogeography*, *23*(5), 574–584. https://doi.org/10.1111/geb.12141

Toussaint, A., Charpin, N., Brosse, S., & Villéger, S. (2016). Global functional diversity of freshwater fish is concentrated in the neotropics while functional vulnerability is widespread. *Scientific Reports*, *6*(1), 1–9. https://doi.org/10.1038/srep22125

Toussaint, A., Charpin, N., Beauchard, O., Grenouillet, G., Oberdorff, T., Tedesco, P. A., Brosse, S., & Villéger, S. (2018). Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. In M. Vila (Ed.), *Ecology letters* (Vol. *21*, pp. 1649–1659). Blackwell Publishing Ltd. https://doi.org/10.1111/ele.13141

Tsou, C.-S. (2022). *nsga2R: Elitist non-dominated sorting genetic algorithm*. https://CRAN.R-project.org/package=nsga2R

Villéger, S., Blanchet, S., Beauchard, O., Oberdorff, T., & Brosse, S. (2011). Homogenization patterns of the world's freshwater fish faunas. *Proceedings of the National Academy of Sciences*, *108*(44), 18003–18008. https://doi.org/10.1073/pnas.1107614108

Weyl, O. L. F., Daga, V. S., Ellender, B. R., & Vitule, J. R. S. (2016). A review of Clarias gariepinus invasions in Brazil and South Africa. *Journal of Fish Biology*, *89*(1), 386–402. https://doi.org/10.1111/jfb.12958

Zhao, Y., Zhang, L., Wang, C., & Xie, C. (2020). Biology and ecology of grass carp in China: A review and synthesis. *North American Journal of Fisheries Management*, *40*(6), 1379–1399. https://doi.org/10.1002/nafm.10512

BIOSKETCH

Rafael Muñoz-Mas is interested in multiple aspects of the management of freshwater ecosystem, including environmental flows assessment and implementation. The research of Rafael Muñoz-Mas has also focussed on the redevelopment of predictive models aimed at forecasting the effect of climate change and ecosystem management on native and invasive freshwater fish species.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Muñoz-Mas, R., Essl, F., van Kleunen, M., Seebens, H., Dawson, W., Casal, C. M. V., & García-Berthou, E. (2023). Two centuries of spatial and temporal dynamics of freshwater fish introductions. *Global Ecology and Biogeography*, *32*, 1632–1644. https://doi.org/10.1111/geb.13714